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BRIEF REPORT

Visual adaptation of the perception of "life": Animacy is a basic perceptual dimension of faces

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Abstract One critical component of understanding another's mind is the perception of "life" in a face. However, little is known about the cognitive and neural mechanisms underlying this perception of animacy. Here, using a visual adaptation paradigm, we ask whether face animacy is (1) a basic dimension of face perception and (2) supported by a common neural mechanism across distinct face categories defined by age and species. Observers rated the perceived animacy of adult human faces before and after adaptation to (1) adult faces, (2) child faces, and (3) dog faces. When testing the perception of animacy in human faces, we found significant adaptation to both adult and child faces, but not dog faces. We did, however, find significant adaptation when morphed dog images and dog adaptors were used. Thus, animacy perception in faces appears to be a basic dimension of face perception that is species specific but not constrained by age categories.

Keywords Social cognition · Face perception · Animacy · Face adaptation

Introduction

Quick, accurate decisions about which objects in the visual field are alive and capable of action are critical for survival. Visual cues that contribute to perceiving an object as "biological" also carry significant social information. The human visual system is tuned to social objects, including faces (Kanwisher & Yovel, 2006), bodies (Peelen & Downing, 2007), and biological motion (Pelphrey & Carter, 2008). Faces, in particular, capture and hold our attention (e.g., Langton, Law, Burton, & Schweinberger, 2008; Ro, Russell, & Lavie, 2001), whether they are real people, dynamic movies, veridical representations, or schematic drawings. This privileged response to socially relevant stimuli persists even when it is suboptimal. For instance, the addition of eyes to otherwise nonbiological objects creates a profound sense of *animacy* that can interfere with task-relevant cues (Gao, McCarthy, & Scholl, 2010). At some point, however, basic detection of a biological agent must yield to an assessment of whether that agent is capable/worthy of social engagement. Distinguishing social from nonsocial objects is fundamentally important to our ability to function in the social world.

Faces provide salient and informative cues for determining animacy and sociability (Balas & Horski, 2012; Looser & Wheatley, 2010). Face animacy is perceived categorically; a steep shift in perception results from gradual morphing between real and artificial face images (Looser & Wheatley, 2010). Furthermore, people are more sensitive to appearance changes near the point of subjective equality (PSE; the point of maximal animate/inanimate ambiguity), and animacy judgments track with judgments about whether faces have other socially relevant characteristics, such as having a "mind," the ability to plan, and the ability to engage in social interactions (Gao et al., 2010; Gao & Scholl, 2011; Looser & Wheatley, 2010). These findings suggest two important things. First, the perception of animacy is closely tied to the perception of others as socially capable beings. Second, animacy may be a separable dimension of faces—like gender and age. If so, animacy may be a property of faces coded for by a separable neural population.

Face aftereffects are an effective way to investigate the processes underlying face perception and recognition (Webster & MacLeod, 2011). High-level visual adaptation has helped characterize many dimensions of faces, including identity (G. Rhodes & Jeffery, 2006), gender (Webster, Kaping, Mizokami, & Duhamel, 2004), and age (O'Neil & Webster, 2011; Schweinberger et al., 2010). These aftereffects

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are thought to primarily reflect neural changes at face-specific levels of visual processing, since adaptation effects transfer across changes in image position, size, and orientation (Leopold, O'Toole, Vetter, & Blanz, 2001; G. Rhodes, Jeffery, Watson, Clifford, & Nakayama, 2003; Watson & Clifford, 2003; Zhao & Chubb, 2001). Adaptation aftereffects result from a reduction in the response of particular subpopulations of neurons tuned to the properties of the adapting stimulus. In the case of faces, adaptation aftereffects can demonstrate that the population of neurons coding facial characteristics is sensitive to a particular dimension, especially if adaptation effects can be transferred across identities or face categories.

We used a high-level adaptation paradigm to ask two questions regarding how face animacy is coded in the visual system: Is animacy a dimension of face perception? Is animacy represented in a category-specific fashion, or is animacy perception across face categories supported by a common neural mechanism?

Experiment 1: Will animacy show adaptation that transfers across individuals?

Method

Participants

Twenty-four young adults (9 female; mean age: 21.9) from the MIT and NDSU communities participated in Experiment 1. All participants had normal or corrected-to-normal vision.

Stimuli: Animacy morphs

Four grayscale images of adult female Caucasian faces with neutral expressions were morphed with visually similar images of doll faces using FantaMorph software (Version 4; Abrosoft Co., Beijing, China). FantaMorph interpolates two original images to create morph continua of images that range from fully human to fully inanimate (Fig. 1). Each continuum consisted of 11 images, spanning real to artificial appearance in 10 % increments.

Procedure

Experiment 1 consisted of two parts: a baseline phase, followed by an adaptation phase. In the baseline phase, participants rated the animacy of 220 face images (two continua from the full set of four) presented in a randomized order. Each stimulus was presented for 1,000 ms, and participants rated each image 10 times over the course of the baseline testing, using a 1–7 scale, where 1 was *completely inanimate* and 7 was *completely human*. We counterbalanced morph pair combinations across participants.

In the adaptation phase, participants were first presented with either a fully human or fully artificial face for 30 s. We selected this adapting face from one of the two continua not seen during the participants' baseline phase. After this extended adaptation period, participants made animacy judgments, using the same procedure as that used during the baseline phase, with the exception that each trial was preceded by a 2-s "top-up" adapting stimulus. We used the same adapting face for the entire adaptation phase. Test stimuli belonged to the morph continua not presented during the baseline phase. To minimize the contribution of image-level adaptation effects, we presented adapting stimuli at a larger size (12° × 12° visual angle) than the test stimuli (4.85° × 4.85°).

Results

We transformed participants' 1–7 rating to a 0–1 scale (without normalizing their range of responses) so that we could estimate the PSE by fitting a psychometric function to each participant's data (see Fig. 2). We fit logistic functions to each participant's normalized ratings using the MATLAB Palamedes toolbox (Prins & Kingdom, 2009) and calculated each participant's aftereffect size (see Fig. 3) by subtracting the adapted PSE from the baseline PSE. The adapted PSE should move toward the adaptor; for example, if the adapting image was a doll, doll faces should look more human postadaptation. Thus, if face animacy is "adaptable," PSE shifts should be in the opposite direction for adaptation to a human face versus a doll face. PSE shifts in the expected direction were expressed as positive numbers, while shifts in the opposite direction were expressed as negative numbers. This allowed us to collapse across doll and human adaptors by comparing the measured PSE values with zero in all cases. Because we have an a priori expectation for the direction of adaptation aftereffects, one-sample t-tests examining these aftereffects were done using a one-tailed t-test.

Adaptation aftereffects were significant when collapsed across human and doll adaptation trials [$t(23) = 4.04$, $p = .001$, one-sample t-test; $d = 1.27$], and the strength of adaptation did not differ for human or doll adapting images [$t(22) = 0.73$, $p = .468$, two-sample t-test; $d = 0.302$]. Additionally, since the adapting face belonged to one of the two morph continua tested during the adaptation phase, we also asked whether adaptation was stronger when adaptor and test image were identity matched. Both continua showed significant adaptation effects that did not differ from one another [$t(22) = 0.668$, $p = .51$, paired-sample t-test; $d = 0.227$], suggesting that animacy adaptation is neither image specific nor identity specific.

Discussion

In Experiment 1, we observed animacy aftereffects obtained for morphed images of adult faces and dolls. In Experiment 2,

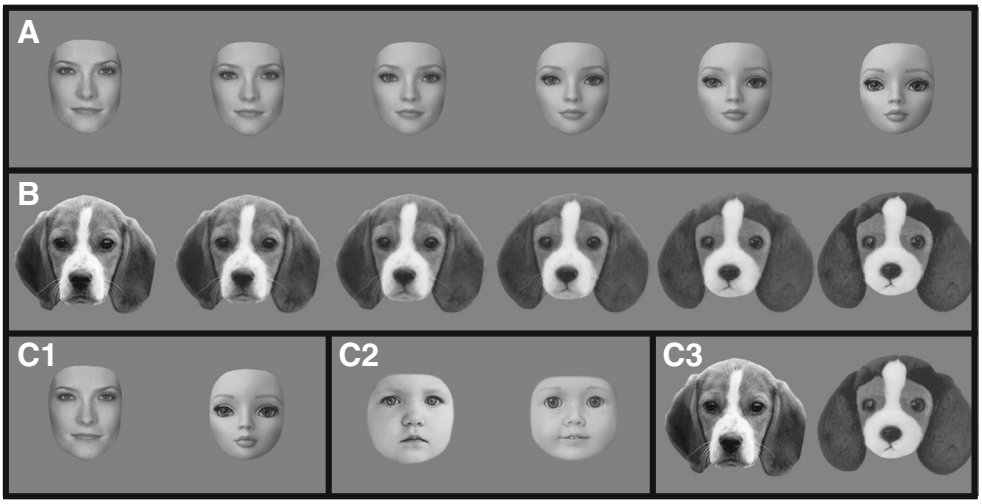

Fig. 1 Examples of **a** adult and **b** dog face pairs used in Experiments 1–3 to create morph sequences. Eleven morph levels evenly spaced along the morph sequence for each face pair were used in the experiments. **c** Examples of adaptors used in Experiments 1–3

we examined the transfer of animacy adaptation aftereffects between child faces and adult faces. The "other age" effect (M. G. Rhodes & Anastasi, 2012) demonstrates that child and adult faces are processed differentially and may be represented by distinct neural subpopulations, as suggested by previous adaptation studies (O'Neil & Webster, 2011; Schweinberger et al., 2010). If animacy perception is category specific, adapting to young children's faces or to dolls that look like

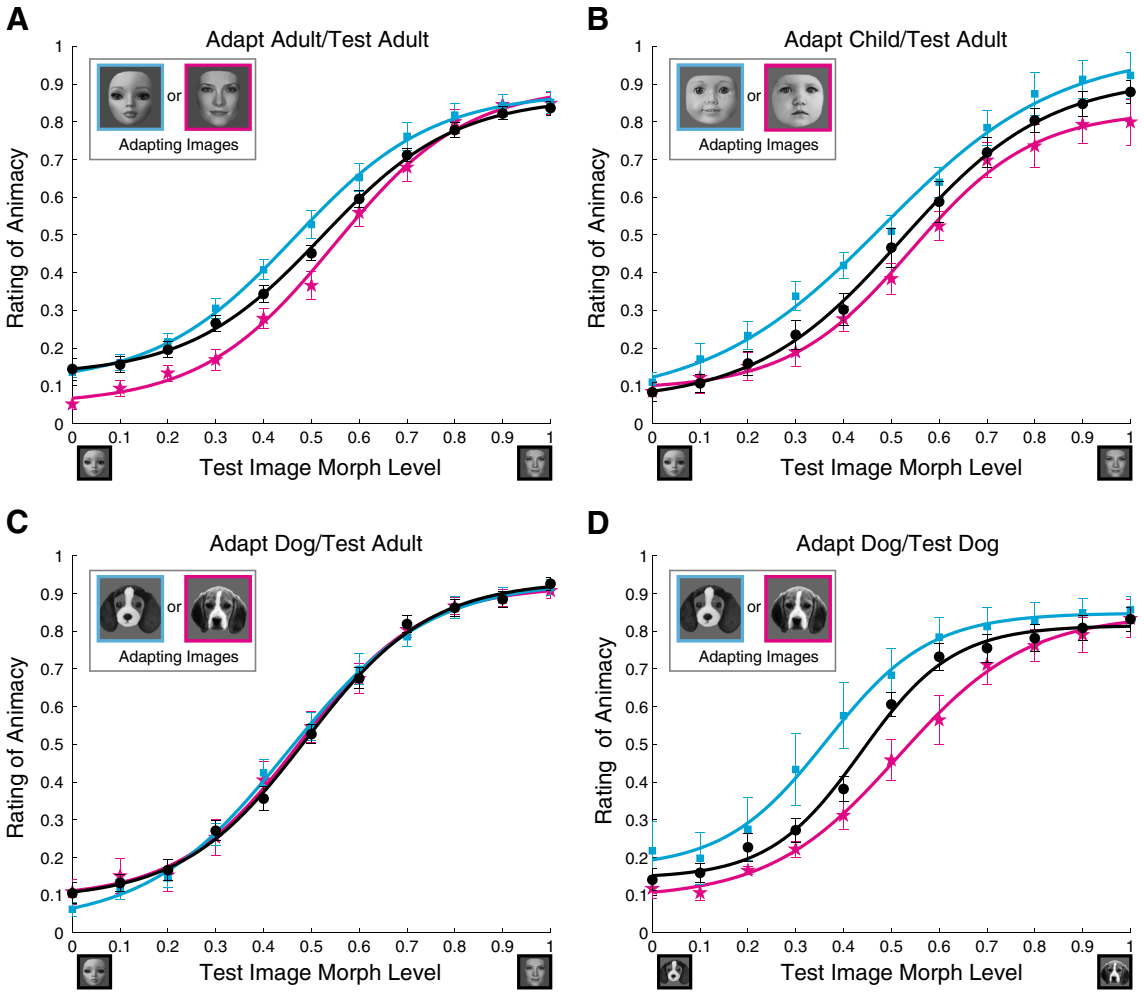

Fig. 2 Average psychometric curves for animacy ratings in each experiment (a–d). In each case, black lines indicate the average *baseline* animacy rating, blue (*squares*) and magenta (*stars*) lines represent postadaptation response following adaptation to a real or toy face, respectively. Error bars = ±1 *SEM*

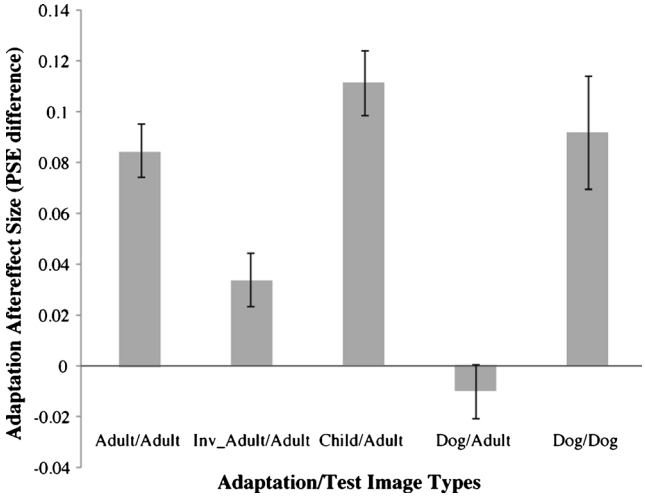

Fig. 3 Average aftereffect size for all four experiments. We observe significant animacy aftereffects in all tasks, with the exception of transfer between dog and human faces. Error bars = ± 1 *SEM*

children should not affect the perceived animacy of adult faces. If, however, animacy is a face characteristic that adapts within face space regardless of age category, aftereffects from child faces should be as strong as those seen to adult faces.

Experiment 2: Will animacy aftereffects transfer between different categories of human faces?

Method

Participants

Sixteen young adults (9 female; mean age: 26.6) from the MIT community participated in Experiment 2. None of these participants were participants in Experiment 1.

Stimuli: Animacy morphs

Stimuli were created as described in Experiment 1. In addition to the four adult morph continua, four grayscale images of young Caucasian children's faces with neutral expressions were morphed with visually similar images of childlike doll faces.

Procedure

We used the same testing procedure as that described in Experiment 1, except that, after baseline animacy ratings were obtained using the adult human/doll morphs, the adaptor used during the adaptation phase was either a real child's face or a childlike doll. As in Experiment 1, the adult morph pairs used during the baseline phase were different from those used during the adaptation phase, and pairs were counterbalanced across participants. In addition, the morph pair from which the adaptation image was drawn was counterbalanced across participants.

Results

Adaptation aftereffects were significant when collapsed across child and doll adaptation trials [$t(15) = 6.96$, $p < .001$, one-sample t-test; $d = 1.76$] and were also significant for adaptation to both human child faces [$t(7) = 5.5$, $p = .001$, one-sample t-test; $d = 1.94$] and doll faces [$t(7) = 5.6$, $p = .001$, one-sample t-test; $d = 1.96$] separately. Animacy adaptation thus exhibits transfer across age categories, suggesting a shared neural mechanism supporting perceived animacy.

Discussion

Our first two experiments revealed that animacy "adapts" and transfers across age categories. Next, we examined the transfer of animacy aftereffects between dog faces and adult human faces to determine whether animacy perception is species specific. If animacy aftereffects are driven by how generally "alive" a face appears to be, adaptation to a dog's face or the face of a stuffed dog toy may also show transfer to adult human faces. If, however, animacy adapts within a species-specific face space, as might be expected from the "other-species effect" (Pascalis, De Haan, & Nelson, 2002; Sugita, 2008), animacy aftereffects may not cross the species barrier. In separate tasks, we examined the extent to which animacy aftereffects transferred between dog adaptors and human test images (Experiment 3a) and also whether or not animacy aftereffects were evident using dog faces as adapting *and* test stimuli (Experiment 3b).

Experiment 3: Will animacy aftereffects transfer across species?

Method

Participants

Sixteen young adults (8 female; mean age: 19.2) from the NDSU community participated in Experiment 3a, and an additional 16 (7 female; mean age: 25.2) from the MIT community in Experiment 3b. None of these participants were tested in either previous task.

Stimuli: Animacy morphs

We created morph continua as described in Experiment 1. In addition to the other morph continua already described, four grayscale images of dog faces were morphed with visually similar images of plush dog faces.

Procedure for Experiment 3a

We adopted the same procedure as that described in Experiment 1, except that after baseline animacy ratings were obtained using the adult human/doll morphs, the adaptor image used during the adaptation phase was from either of the extreme ends of the dog/stuffed-toy continua. As in Experiment 1, the adult morph pairs used during the baseline phase were different from those used during the adaptation phase, and pairs were counterbalanced across participants. In addition, the morph pair from which the adaptation image was drawn was counterbalanced across participants.

Procedure for Experiment 3b

When within-species adaptation was tested using the dog/toy morphs, the procedure was exactly as described in Experiment 1, except that the dog/toy morphs were used instead of the human/doll morphs. In addition, participants were asked to rate dog/toy morphs as either "fully dog-like" or "fully toy-like."

Results and discussion

Adaptation to dog/toy dog faces did not produce a significant adaption aftereffect when human/doll morphs were the test items [$t(15) = -0.48$, $p = .64$, one-sample t-test; $d = 0.12$]. However, animacy aftereffects were obtained when both the adaptor and test images were dogs [$t(15) = 2.15$, $p = .025$, one-sample t-test; $d = 0.54$]. Thus, while facial animacy *is* adaptable within nonhuman species, animacy aftereffects do not transfer between different species.

Experiment 4: Will animacy adaptation aftereffects be seen in inversion?

Experiment 4 examined whether animacy adaptation aftereffects would still be seen if the adapting stimulus was inverted. If animacy adaptation aftereffects rely on face-specific mechanisms in face space, they should be weaker when the adapting stimulus is inverted.

Method

Participants

Twenty-four young adults from the MIT community (13 female; mean age: 24.3) participated in Experiment 4. None of the participants in Experiment 4 were tested in Experiment 1, 2, or 3.

Stimuli: Animacy morphs

Stimuli were the same as those described in Experiment 1.

Procedure

The testing procedure was exactly as described in Experiment 1, except that, after baseline animacy ratings were obtained, the adaptation image used during the adaptation phase was inverted.

Results and discussion

Animacy ratings were transformed as described for Experiment 1 to obtain each participant's PSE for both baseline and adaptation conditions. Adaptation to inverted faces did produce an aftereffect that was very close to significant [$t(23) = 1.6$, $p = .06$, one-sample t-test; $d = 0.327$]. Despite the fact that we do see near-significant adaptation aftereffects to an inverted face, the adaptation aftereffect seen to the inverted faces was significantly weaker than that seen to upright faces [$t(46) = 2.1$, $p = .04$, two-sample t-test, two-tailed; $d = 0\ .61$].

General discussion

Our results revealed reliable adaptation aftereffects in the perception of animacy in human faces. Following adaptation to either a wholly inanimate doll face or a fully human face, the perceived animacy of subsequently presented faces was shifted away from the adapting stimulus, consistent with other examples of face adaptation. These animacy aftereffects were significantly weaker when the adapting stimulus was inverted, demonstrating that at least part of this aftereffect may be face specific. These results demonstrate that the perception of animacy in faces is flexible and can be tuned, even over a very short time scale, by experience—thus suggesting that animacy is a psychologically real dimension of face variability.

Our data further demonstrate significant adaptation across age groups (child vs. adult), suggesting that animacy adaptation transfers not only across different identities (as demonstrated in Experiment 1), but also across different face *categories* (demonstrated in Experiment 2). The transfer of adaptation effects across categories has a limit, however, since the results of Experiment 3 show that adaptation effects do not transfer between faces of different species.

What cues may be driving these animacy adaptation aftereffects? Although our data suggest that animacy adaptation is a high-level aftereffect, it is difficult to disentangle the visual cues that may contribute to the effect. Two cues that could drive part of this adaptation effect are skin texture and the reflective qualities of the eyes. Adaptation aftereffects to

manipulations of surface texture/reflectance have previously been demonstrated in nonface objects (Motoyoshi et al., 2007) and could explain some of the adaptation effect seen in our data. The clear difference in adaptation strength between upright and inverted adaptors, however, suggests that surface-based cues alone cannot explain the entire effect. Shape-based cues may also drive part of this effect. Although doll and human faces did not differ from each other systematically across morph pairs, certain differences remained relatively stable—for example, dolls' eyes tended to be slightly bigger and lower in the face than those of real human faces. These sorts of shape-based cues may be similar to previously reported shape-based manipulations of faces (e.g., expansion/contraction of face features) that have shown adaptation aftereffects on the perception of facial characteristics like "normalcy" and "attractiveness" (e.g., G. Rhodes et al., 2003). It is important to note, here, that we tested the transfer of adaptation effects across age and species categories only in one direction (child to adult, dog to human), leaving open the possibility that adaptation transfer in the other directions might differ. Although the one-way nature of these tests does not undermine our conclusions, investigating adaptation effect transfer in the other direction may provide clues to the source of these effects, especially if they prove to be asymmetrical. More generally, a systematic investigation of the contribution of both surface/texture and shape-based cues to animacy aftereffects will be important in future research investigating the perception of face animacy.

What do these results tell us about face perception itself? First, our data suggest that animacy is a *perceptual* dimension of faces, susceptible to high-level adaptation, thus lending additional support to earlier evidence that the human face processing system includes sensitivity to the animacy of faces (Balas & Horski, 2012; Looser & Wheatley, 2010). Second, the observed transfer between child faces and adult faces suggests that, while child faces are farther from the norm for adult observers than adult faces, they are still represented in the same face space as adult faces and that changes in animacy are perceived similarly across the two age categories. Animacy is not, however, perceptually monolithic. The lack of transfer between human and dog faces both reassures us that the effect is unlikely to be the result of response bias and reinforces the perceptual nature of the effect; if the effect relied on the "concept" of animacy, we might expect to see transfer of adaptation from dogs to humans. Perceptually, animacy in human faces and dog faces may be supported by different visual cues; texture, surface reflectance, and shape cues may still be relevant to the perception of animacy in dog faces, but in a quite different way than in human faces. In addition, our results are consistent with a model in which dog faces are not represented in the same face space as human faces but may be represented in a face space of their own.

What does animacy adaptation tell us about the neural architecture of the face-processing system? Previous research demonstrated that differences in the processing of human and doll faces did not emerge until relatively late in perceptual processing (~400 ms) (Wheatley, Weinberg, Looser, Moran, & Hajcak, 2011) and may take place in face-sensitive regions of the superior temporal sulcus (STS; Looser, Guntupalli, & Wheatley, 2012). Our data cannot directly address the question of where animacy may be coded in the brain, but in the context of these previous results, our data suggest that processing differences between animate and inanimate faces may be driven by face-selective neural populations within the STS that drive animacy perception. If so, animacy perception in faces may also be related to the perception of animacy in other social stimuli that engage the pSTS, including both point-light human figures engaged in "biological motion" (e.g., Grossman, Jardine, & Pyles, 2010) and simple animated shapes whose movements are perceived to have intention (Gao, Scholl, & McCarthy, 2012; Lee, Gao, & McCarthy, 2012). Further research is needed to clarify whether animacy perception in faces and biological motion perception engage similar brain regions and whether adaptation effects using biological motion stimuli (Jordan, Fallah, & Stoner, 2006; Troje, Sadr, Geyer, & Nakayama, 2006) can also reflect differences in animacy (for instance, contrasting adaptation effects to the movements of a humanoid robot against typical human movements). Regardless of its neural substrate, our results demonstrate that changes in animacy activate and adapt the tuning of the neurons that underlie face perception—at the very least suggesting that animacy perception is a fundamental part of the face-processing system.

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